

Bonn. zool. Beitr.	Bd. 42	H. 3-4	S. 225—236	Bonn, November 1991
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Reproduction and social organization in *Peropteryx kappleri* (Chiroptera, Emballonuridae) in Colombia

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Abstract. The social organization and reproduction of *Peropteryx kappleri* were studied in small colonies inhabiting a series of abandoned coal mines at the base of the Western Andes near Cali, Colombia. All bats from each colony were individually marked and observed frequently for extended periods during both day and night. With few exceptions, all adult bats left the mines alone or in small groups shortly after 1800 h and returned between 0200 and 0600 h. Only one social group was found in each mine and these groups demonstrated high fidelity, not only to their mines of residence but also to particular preferred sites within them. Males did not exhibit territorial behavior and females dominated the organization of the social groups. Some individuals, usually females, occasionally visited other mines nearby, but always returned to their own social groups. The birth of young coincided with the two rainy seasons in this tropical region and some females bore young in both seasons during the year of observation. In the final days of the gestation period, females left the group to establish individual breeding territories some distance away from the rest of the group members. These sites were continuously maintained for parturition and rearing of the single young until weaning. From the day of birth, the young were invariably left alone in this territory during the night while the mothers were absent from the mine. After weaning, between 50 and 60 days of age, the young dispersed from the mines and the females returned to their position in the social group.

Key words. *Peropteryx kappleri*, reproduction, social organization, Colombia.

Introduction

Bats are among the most gregarious of all mammals, forming colonies of several million individuals in the case of *Tadarida brasiliensis* in the southwestern United states (Humphrey 1971). This colony life has favored the development of complex social systems among Neotropical emballonurids, such as the harems maintained by single territorial males in *Saccopteryx bilineata* (Bradbury & Emmons 1974), or phyllostomids such as *Artibeus jamaicensis* (Morrison 1979).

The evolution of social behavior is governed by environmental features such as suitable roosts and food resources (Bradbury 1977). For this reason, species of the same genus may show different social systems. Social factors may vary among species and take many diverse forms (Hill & Smith 1984). The size of social groups depends on local abundance of suitable resting places as hollows in rocks (caves, mines), trees or old buildings (Hill & Smith 1984; Fenton 1985). A habitat with limited roosting sites limits the development of large colonies (Kunz 1973). Emballonurids are agile bats, crawling and scampering on the walls of their preferred caves and tree trunks (Hill & Smith 1984).

It has been demonstrated that tropical chiropterans have a variety of social organizations (Dwyer 1971; Bradbury 1977) involving complex responses to seasonal environmental changes (McWilliam 1987). Little is known about social structure and

functioning for the tropical species (Bradbury 1977) largely as a result of the difficulty of making direct observations within dark caves (McWilliam 1987). There have been few studies of adaptation to climatic changes in the tropics involving comparisons between climate, reproduction, growth and social organization except for those presented for *Brachyphylla cavernarum* (Nellis & Ehle 1977) and *Coleura afra* (McWilliam 1987). This paper reports some observations on the social organization and reproduction of *Peropteryx kappleri* (Emballonuridae) and compares this with other species.

Material and methods

The study was conducted in a series of seven abandoned coal mines (Table 1) located near the base of the Western Cordillera of the Andes, west of Cali, Departamento del Valle, Colombia (3° 27' N, 76° 32' W) between November 1981 and December 1982. All results are from natural populations of *Peropteryx kappleri* roosting in the coal mines. Colonies in other nearby mines were also observed during the study, but could not be visited on a regular basis because of difficult access. The mostly horizontal mine shafts, from 10 to 200 m in length, were usually cool and humid even during the dry seasons. The mean inside temperature was from 20.8 °C to 22.4 °C and the ceiling height varied from 1.5 to 3.0 m. During 1982, the total annual rainfall was 1767 mm with peaks in the months of April and November, mean relative humidity was 73 %, and the annual mean temperature was 24.5 °C (Universidad del Valle Station, ca. 2–5 km from the mines studied, HIMAT 1987). The vegetation of the region is described as Tropical Dry Forest (bs-T, Espinal 1977).

Individuals of *P. kappleri* were captured in their roosts by hand or by hand net both day and night. Most bats were marked with colored plastic rings (3 mm in diameter and 5 mm long) hung on a loop of colored paraffin-coated thread tied around their necks as a collar. Individuals where differentiated by the combination of colored rings and thread color differed between caves (Fig. 1).

During the day observations and data recording at their roosts, a mist net was placed at the cave entrance to prevent escape. Sometimes nets were also placed during the night to capture other bat species that share the roost site with *P. kappleri*. Some of the larger mines supported small populations of *Glossophaga soricina*, *Carollia perspicillata* and *Desmodus rotundus* in addition to *P. kappleri*. Data recorded for each bat included: sex, body weight, forearm length, reproductive condition, and exact roosting site in the mine.

Thirty-eight young born during the study were frequently measured and weighed using a dial caliper and spring balance during a period of ca. 60 days, the time interval necessary to reach adult size. Measurements were taken during the night, between 2000 and 2100 h, when

Table 1: Characteristics of seven abandoned coal mines harboring populations of *Peropteryx kappleri*, including numbers of adults captured and young born in each mine during the period from November 1981 to December 1982 (All measurements for mines in m, except temperature, in °C).

Mine	Elevation	Length	Average Height	Average Width	Average Temp. $\bar{x} \pm SD$		Adults			Young	
							♂	♀	♂	♀	?
1	1,190	15	2.0	1.5	22.0	0.2	10	14	0	3	1
2	1,220	30	1.5	1.0	22.3	0.8	3	2	0	1	
3	1,415	>200	3.0	1.8	20.8	0.5	14	33	2	10	2
4	1,390	>200	2.5	3.0	21.0	0.6	8	7	3	3	
5	1,230	10	1.5	1.5	21.4	0.5	2	8	0	4	
6	1,315	15	2.0	2.0	21.4	0.6	13	13	4	3	
7	1,320	15	2.5	2.5	21.6	0.5	6	10	5	0	
Total							56	87	14	24	3

the adults were absent from the mines foraging. Neonates were identified by relating their roosting positions to numbered markers and topographic features during the first 15 days after which they were marked with colored rings, the string collars being changed every 5–8 days.

Daily activity patterns inside the mines were studied by direct observation using a head lantern. For this purpose a black plastic blind was hung along one end of the cave corridor with a hole in the upper portion where the observer could stand without disturbing the bats. Records of sex, weight and arm length were taken during each visit. Caves were visited on a weekly basis and daily during the reproductive period. Notes on climate were also taken.



Fig. 1: Adult male *Peropteryx kappleri* roosting during the day in mine #6, showing the individual marking system with colored plastic rings.

Results

Roosts and daily activity patterns

The seven abandoned coal mines contained colonies formed by from 5 to 47 individuals of *Peropteryx kappleri* (Table 1). They were found to roost in the darker portions of the mine shafts just beyond the point where the intensity of light from the entrance was insufficient for human vision during the day, either in the deeper portions of short mines or in side tunnels. They roosted as groups of individuals, each maintaining a minimum individual distance, on the walls of the mine (Fig. 2) or, preferentially, in cupolas formed in the ceiling by cave-ins.

During the day, most individuals occupied precise resting positions within a cluster. A few solitary individuals were found in fixed sites on the periphery, not forming an integral part of the group. The roosting positions were maintained during the entire 14 months of observations with some temporary movements from one mine to another. One female occupied a solitary site at the rear of mine #2. This female was the individual most frequently observed to visit other roosts (she was



Fig. 2: Group of adult *Peropteryx kappleri* roosting on a concave mine wall. The open wings are a sign of alertness, indicating readiness to fly.

found not to be at her roosting site on seven occasions). She also gave birth and reared her young in the same site at the back of the mine.

Evening emergence began at 1800 h and was normally completed in less than one hour. *P. kappleri* became active at 1600 h, at which time bats began to vocalize and make flights to near the entrance and back to the deeper parts of the mine shaft. Most bats left the day roost in small groups of three to five individuals. Approximately 20 % of the bats left the mines unaccompanied. *P. kappleri* normally remained outside the cave during the entire night. Only five males and one female (with young) were observed inside the mines at this time. Bats usually returned in groups to their roosts between 0200 to 0600 h. They approached the mine entrance in groups and showed aggressive interactions with their mouths, giving the appearance of biting each other while flying. After several passes, females were usually the first to enter. Inside the cave their flight was accompanied by strong vocalizations, especially when approaching one another, until they finally settled on their roost sites. Each individual maintained the same roosting site and changes were very rarely observed. Self-grooming was the next activity after roosting. The fur was combed with the claws of the hind foot. Wings were stretched out, first one then the other, repeated several times. This grooming activity lasted until about 0800 or 0900 h. Mutual grooming was never observed among the adults of a social group, although it occurred between mother and young.

Social groups

A total of 143 individuals of *P. kappleri* was observed in the seven roosts studied (Table 1). Individual mines supported from 5 to 47 individuals, including residents

and temporary visitors. In each colony, groups made up of both males and females were found. Summing colonies from all mines, adult females outnumbered males (by a factor of 1.4), suggesting harem formation. A total of 36 individuals (25 females, 11 males) was observed to visit other roosts, either being found in another of the seven mines included in the study (13 females, 4 males) or simply absent from their known roosts, presumably visiting others nearby (12 females, 7 males). All visitors later returned to their original roosts and social groups. Compared to the size of the social groups, a relatively small proportion of individuals (12 % of residents) moved between roosts. *P. kappleri* exhibited a stable conformation of core social groups during the 14 months of observation. *P. kappleri* males were not observed to defend territories and social groups usually contained more females than males.

Juvenile *P. kappleri* of both sexes dispersed from the roosts where they were born after the eighth week. Never during the 14 months of the study was a juvenile observed to stay, integrating itself into the social group of its mother.

Reproduction

Births occurred during January, March, April, May, October and November, with a marked peak in April and a smaller one between October and November (Fig. 3), corresponding to precipitation peaks for 1982 (HIMAT 1987). Rainfall in these peak months was above the 30 yr average for nearby Palmira (1006 m) and Miranda (1200 m), which show the same bimodal precipitation pattern (FAO 1985). The total number of juveniles born was 41 (23 females, 15 males, and 3 of unknown sex). This synchronized parturition appears to be the result of a highly synchronous copulation behavior. On 20 June 1982 at 1000 h in a nearby mine not included in this study,

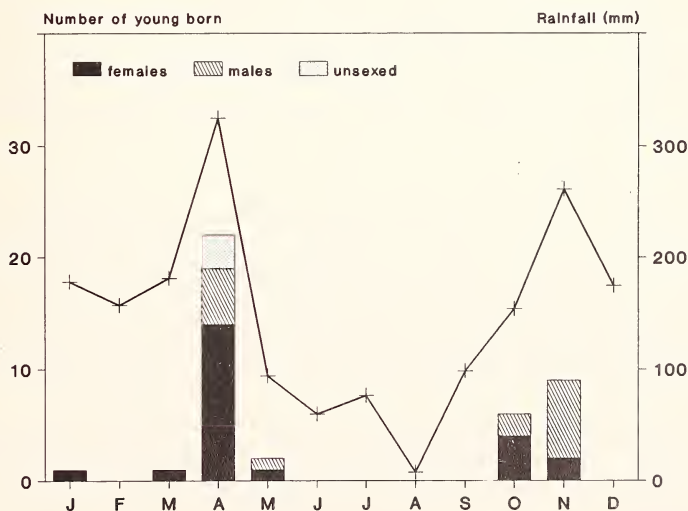


Fig. 3: Total number of young *Peropteryx kappleri* born in all seven mines studied during 1982 and total monthly rainfall during 1982 (data from HIMAT 1987).

which contained more than 60 individuals of *P. kappleri*, three pairs were observed mating ca. 50 cm from one another, surrounded by a larger group at rest.

When females were close to parturition, an increase in body weight of 1–2 g was observed. At this time they moved to different individual roosting sites, away from the group but inside the same mine shaft. They tended to roost in general proximity, but maintaining a distance of at least one meter between each other. After weaning their young, the adult females rejoined the social group to which they initially belonged. The weaned young, having achieved adult size apparently dispersed from the roosts and were never observed again.

Of the 87 females, 38 (44 %) reproduced during the 14 month study period, always with a single young per litter. Four females had two litters during 1982. Each female gave birth to two young of the same sex (two to males and two to females).

Maternal care

During the day, *P. kappleri* females were always found together with their young in their individual roosting sites and the bond between mother and infant was maintained from birth until weaning. Young were always observed hanging alone during the night when the mothers were absent, even on the day of birth. On two separate occasions, one in each peak of reproductive activity, new-born were found alone at the roost site.

Communication between the mother and new-born was done through audible vocalizations. Females returning from foraging emitted a call which was answered by vocalizations from the young. These vocalizations continued until the young could attach itself to its mother. These mother-baby vocalizations have also been reported for various microchiropteran species (Hill & Smith 1985). When mother and young were separated, it took less than five minutes for the mother to recover its young.

During the day, the mothers covered the young with their wings and the young bats attached themselves to their mothers' hair at the base of the tail using the claws of their feet while they nursed. If disturbed, females would open their wings to the side as if to fly or fly to a new site within the mine with the young attached.

Growth and development

On the day of birth, a piece of umbilical cord was observed to remain only into the first night. The new-born had their eyes open and they closed them when exposed to the light. The wings were brilliant dark black and clumsy. Wet hair was present only on dorsum, the abdomen being completely naked and the internal organs visible through the pink skin. The toes were separate and similar to those in the adults, with some long hairs over the tarsi. The new-born were defenseless and their only activity was to nurse.

The new-born were very strong; from the first day it was difficult to separate them from their mothers. Their vocalizations were barely audible. The minimum weight recorded for a new-born was 1.5 grams and the minimum forearm length was 20 mm (female). On the third day after birth, the hair was dry, soft and silky. During the fourth day they tried to open their wings as if to fly and vocalizations were stronger. Short jumping flights, advancing no more than one meter, were first observed on the

eighth day while the mother was absent at night. During the day, the mother normally escaped with the young firmly attached if disturbed (Fig. 4). The vocalizations of the young were more clearly defined. After twenty days the young could reach up to two meters in each flying jump; the abdomen presented little hair but the skin was darker. After thirty days the mothers still carried the juveniles to nurse; if disturbed the mother carried the young or it followed the mother, flying to another place. After



Fig. 4: Female of *Peropteryx kappleri* with her approximately eight-day-old young clinging tightly while nursing.

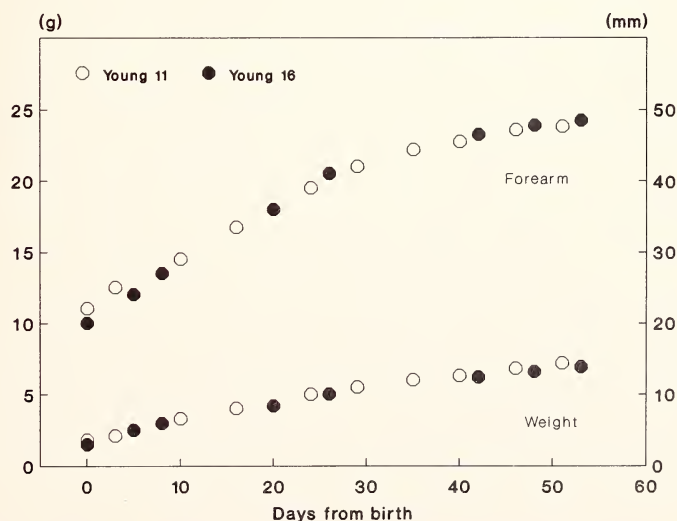


Fig. 5: Growth curves for two female *Peropteryx kappleri* discovered on day of birth (#11 born 18 April, #16 born 16 October 1982).

forty days the juveniles still hung on their mothers for nursing. At this age they were able to fly like an adult.

Approximate adult size (forearm) and weight were reached by fifty-five days of age. At this time we first observed them to leave the roost, supposedly for foraging. During the day they usually hung from 10 to 30 cm from their mothers' roosting site. The only observable difference between juveniles and adults at this stage of development was hair color. In the juveniles the hair was light at the base, darker at the tips and soft and silky, while the hair of adults was more dense. During the study period no external signs of molting were observed. The growth rate was faster in the first month and also was faster in those born in the long rainy season than those born in the short rainy season. After sixty days most of the juveniles of both sexes had abandoned the cave and were never seen again.

Sexual dimorphism was observed in the 143 marked adults of *P. kappleri*. Females had a longer forearm (51.85 ± 1.62 mm) and weighed more (10.21 ± 1.33 g) than males (48.89 ± 1.46 g; 7.89 ± 1.03 mm). In the juveniles observed, this sexual dimorphism was also evident before abandoning the roosts.

Discussion

Peropteryx kappleri requires more protected roosting sites than those used by some other species of emballonurid bats. Under natural conditions *P. kappleri* prefers humid caves and rocky fissures (Sanborn 1937; Villa-R 1966; Handley 1976). Such sites are generally selected by bat species for microclimatic conditions that favor gestation, nursing, development of young and protection from predators (McNab 1974; Humphrey 1975).

In the study area, *P. kappleri* roosts in abandoned coal mines common at the base of the Western Cordillera of the Andes on the outskirts of the city of Cali. The mines studied supported relatively stable populations of between 5 and 47 individuals. However, more than 60 individuals were observed in another mine which was not included in the study. These coal mines are a good approximation of natural roosting places for *P. kappleri* and they were found to be common, even in smaller excavations. Roosts with these conditions may favor the formation of more stable social groups than the exposed branches or tree trunks used by *Saccopteryx leptura* and *Rhynchonycteris naso* (Bradbury & Vehrencamp 1976a) or the hollow tree trunks used by *S. bilineata* (Bradbury & Emmons 1974) and *Artibeus jamaicensis* (Morrison 1979). A cave (or abandoned mine) provides a permanent roost and offers protection against predators which is especially important during reproductive seasons.

P. kappleri had two peaks of reproductive activity in this study. Most births occurred in April with a total of 23 young. The other birth peak was in October–November with 6 and 9 individuals, respectively. Both birth peaks coincided with the rainy seasons. *S. bilineata* in Trinidad have only one period of reproductive activity, with young being born from late May to mid-June, just at the beginning of the rainy season (Bradbury & Emmons 1974). In the present study, *P. kappleri* had two periods of reproductive success, similar to *Coleura afra* in Kenya (McWilliam 1987), suggesting that two reproductive cycles may be the rule for emballonurids in tropical regions with two rainy seasons.

Parturition was synchronous in *P. kappleri* in all seven mines studied. During the long rainy season, 34 % of the females gave birth and during the short rainy season 25 %. Only 7 % of the females reproduced in both rainy seasons. Two births per year have been reported in other neotropical bats (*Artibeus jamaicensis*, Flemming 1971; *Rhynchonycteris naso*, Bradbury & Emmons 1974; *Myotis nigricans*, Wilson 1971), indicating that tropical bats which are not restricted by food availability or climate for long periods tend to exhibit polyestrous reproductive cycles.

Overall more females were born than males (1 : 1.4, males : females) in contrast to *Coleura afra*, another emballonurid, in tropical Africa (McWilliam 1987). The sex ratio among new-born differed between the two reproductive periods: 1 : 3.5 (males : females) during the first wet season and 1 : 0.6 (males : females) for the second. Although our sample size is small, we suggest that the social organization in *P. kappleri*, with females outnumbering males requires more females to be born.

Except for being able to open their eyes at birth, the ontogeny of *P. kappleri* is similar to that reported for several species of vespertilionids (Jones 1967; O'Farrell & Studier 1973). In this respect, they are similar to captive phyllostomids such as *Carollia perspicillata* (Kleiman & Davies 1979) and *Desmodus rotundus*, but gestation and development in the latter species is much slower (Schmidt & Manske 1973).

Females of some bat species carry the juveniles while foraging and/or between roosting sites (Young 1967; Fenton 1969; Davis 1970; Bradbury 1977). Other emballonurid species carry their babies during foraging or leave them in different roosting sites until the adults return (Bradbury & Emmons 1974). Bradbury & Vehrenkamp (1976b) reported that *P. kappleri* females leave the young in the roosting site during their nocturnal foraging bouts. From the present study, we conclude that this is the general rule for *P. kappleri*; females never carry the young during the night, not even on the day of birth. Leaving juveniles in the roosting sites suggests that *P. kappleri* is safe from predators in the coal mines.

The social organization of *P. kappleri* was similar to that reported for *Rhynchonycteris naso* and *Saccolaryx leptura* (Bradbury & Emmons 1974). Males and females maintain individual spacing while roosting on suitable substrates inside the coal mines. In these social groups females usually outnumber males, as also reported for *Myotis nigricans* (Wilson 1971). A few solitary individuals occupy peripheral sites, not forming an integral part of the group, similar to reports for *S. bilineata* and *S. leptura* (Bradbury & Vehrencamp 1976a). The social groups persisted throughout the study period and only one group was present in each mine. Size of the social group and individual positions within it demonstrated a high level of temporal stability. A few resident individuals, 13 females and 4 males, moved from one cave to another, but always returned to their original site, demonstrating high site fidelity for this species. This behavior has also been observed in other species (*Desmodus rotundus*, Wimsatt 1969; *Myotis adversus*, Dwyer 1970; *Carollia perspicillata*, Fenton 1985; *Saccolaryx bilineata*, McCracken 1987), where populations showed frequent interchanges between nearby harems or colonies. We suspect that females might visit other groups in search of other males.

Before parturition, females move from the social group to larger individual roosting sites for birth and growth of young. Even though females change roosting sites temporarily, they return to their specific sites after the juveniles are weaned.

That those females producing two litters during the study period returned to the same individual roosting sites suggests some sort of territorial defense, although we did not observe aggressive encounters between adjacent reproductive females.

A stable group size and composition for *P. kappleri* in each roost site is assured by the dispersal of juveniles after reaching adult size. During the study period, no juvenile was observed to become integrated into its mother's group. This is in contrast to *S. bilineata*, where juveniles stay with their mothers until the third month (Bradbury & Vehrencamp 1976a), and to *Coleura afra* where even three generations of females may be present in a group (McWilliam 1987). During our study, juveniles were never observed after dispersal. Adult female movements and juvenile dispersal may suggest that inbreeding in *P. kappleri* is minimal, as also reported for *S. bilineata* (McCracken 1984).

We have no evidence to suggest that *P. kappleri* males are territorial or compete for females. On the contrary, it appears that females dominate the social structure, entering the roost first after foraging, and choosing the roosting sites for reproduction. Also, the females most frequently moved between roosts. However, males might be involved in controlling group size by promoting the early dispersal of young as reported for *C. afra* (McWilliam 1987) to the extreme.

That *P. kappleri* social organization is not as complex as in other bat species is suggested by the fact that social grooming was never observed except for mother-young grooming. The rather simple and stable social organization in *P. kappleri* is selected for by favorable climatic conditions, abundant seasonal food resources, and secure roost site availability found in this tropical region. *P. kappleri* exhibits a high site fidelity both for day roosting sites and individual reproductive roosting sites.

Acknowledgements

This paper is the result of the research project presented as an undergraduate thesis of the senior author at the Universidad del Valle, Cali, Colombia. The authors express their thanks to all those individuals who participated in the field work, especially B. V. Giral, and to H. Carvajal and C. A. Hoyos who prepared the photographs. We thank R. Hutterer for encouragement to publish the results presented here, for preparation of the graphs, and translation of the abstract to German. L. M. Alvaré is grateful to LUFTHANSA for providing necessary financial support for the revision of recent literature and preparation of the manuscript while at the Alexander Koenig Zoological Research Institute and Museum.

Resumen

La organización social y reproducción de *Peropteryx kappleri* fueron estudiadas por observación directa durante día y noche por el período de un año cerca a Cali, Colombia. Se encontró un sistema social basado en la conformación de grupos estables de tamaño variable de murciélagos que ocupaban socavones de minas abandonadas, probablemente debido a la protección ofrecida contra temperaturas extremas y depredadores. Los grupos sociales ocupaban lugares escogidos dentro de las minas y algunos individuos adultos se mantuvieron solitarios. Generalmente, los murciélagos adultos se ausentaban de la mina desde 1800 h, cuando salían en busca del alimento, hasta entre 0200 y 0600 h del día siguiente. En cada mina se encontró un solo grupo social y los individuos presentaban fidelidad tanto a su mina de residencia como a los sitios preferidos dentro de ella. Los machos no presentaron comportamiento territorial y las hembras dominaron la organización de los grupos sociales. Algunos individuos, usualmente las hembras, visitaron otras minas en ocasiones, pero siempre volvieron a su grupo social. Las épocas de mayor número de partos coincidieron con los dos picos anuales de lluvia. Las hem-

bras parieron una sola cría y algunas se reprodujeron dos veces durante el año de estudio. Durante los últimos días de la gestación, las hembras se alejaron de su posición en el grupo, para establecer territorios individuales en sitios algo apartados. Allí parieron a su cría y permanecieron en este lugar hasta el destete. Desde el día del parto, las crías fueron dejadas solas en estos territorios mientras la madre salía de noche de la mina. El vínculo madre-hijo duró entre 50 y 60 días, después del cual las hembras volvieron a integrarse al grupo social y los juveniles se dispersaron de las minas.

Zusammenfassung

Die Fortpflanzung und Sozialstruktur in kleinen Kolonien der Fledermaus *Peropteryx kappleri* wurde in einer Reihe von aufgelassenen Kohlengruben am Fuß der westlichen Anden bei Cali, Kolumbien, studiert. Alle Fledermäuse dieser Kolonien wurden individuell markiert und regelmäßig über längere Zeiträume tags wie nachts beobachtet. Mit wenigen Ausnahmen verließen alle erwachsenen Tiere die Stollen allein oder in kleinen Gruppen kurz nach 18:00 h und kehrten zwischen 02:00 und 06:00 h zurück. In jedem Stollen wurde nur jeweils eine Sozialgruppe gefunden; die Gruppen bewiesen eine hohe Ortstreue in bezug auf den gewählten Stollen als auch auf die bevorzugten Hangplätze innerhalb der Stollen. Die Männchen zeigten kein Territorialverhalten; die Organisation der Sozialgruppen wurde von den Weibchen bestimmt. Einige Tiere, vorwiegend Weibchen, besuchten gelegentlich Nachbarstollen, kehrten aber immer zu ihrer eigenen Gruppe zurück. Die Geburt der Jungen fiel in die beiden Regenzeiten dieser tropischen Region; einige Weibchen gebaren Junge in beiden Regenzeiten eines Beobachtungsjahres. Am Ende der Tragzeit sonderten die Weibchen sich etwas von der Gruppe ab und bildeten individuelle Brutpflegebezirke. Diese Plätze wurden von der Geburt bis zur Entwöhnung des einzigen Jungtieres beibehalten. Vom Tag der Geburt an wurden die Jungtiere in jeder Nacht in den Weibchenterritorien alleingelassen, nachdem die Mütter die Stollen verlassen hatten. Nach der Entwöhnung, die in das Alter zwischen 50 und 60 Tagen fiel, verließen die Jungen die Stollen, während die Weibchen an ihre alten Positionen innerhalb ihrer Sozialgruppen zurückkehrten.

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Jahr/Year: 1991

Band/Volume: [42](#)

Autor(en)/Author(s): Giral Gloria E., Alberico Michael S., Alvaré Luz Marina

Artikel/Article: [Reproduction and social organization in Peropteryx kappleri \(Chiroptera, Emballonuridae\) in Colombia 225-236](#)